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The Genus *Offadesma* Iredale, 1930 (Bivalvia: Periplomatidae) in the Miocene of Patagonia

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Abstract. The periplomatid genus *Offadesma* Iredale, 1930 was known from a few species found from the middle Eocene to Recent in New Zealand and Australia. Two new records are added from southern South America in Argentina. *Offadesma* sp., represented by a sole specimen from the Monte León Formation (late Oligocene-early Miocene) exposed near Santa Cruz, in southern Patagonia, and *Offadesma isolatum* n. sp., collected at Punta Pardelas (northern Patagonia) in late Miocene rocks referred to the Puerto Madryn Formation. The relationships to other periplomatids from South America seem to be remote, and therefore the migration of *Offadesma* from Australasia to South America during Cenozoic times as a consequence of the onset of the Antarctic Circumpolar Current is proposed.

INTRODUCTION

The family Periplomatidae includes—among others—a number of species known from shelf environments along the Pacific and Atlantic coasts of America and in tropical West Africa. They are generally not very abundant and as fossils they have been recorded occasionally in rocks of different ages ranging from Jurassic to Recent (Harper et al., 2000). Their occurrence—whether living or fossil—is restricted to specialized environments (Morton, 1981b). In addition to their apparently low numbers, the aragonitic nature of their fragile shells conspires also against their preservation.

In southern South America, the family is represented by two extant species, i.e., *Periploma ovatum* d'Orbigny, 1846 and *Periploma compressum* d'Orbigny, 1846. Both species occur along the coast from southern Brazil to northern Patagonia (Ríos 1994). These two species belong in *Periploma* s.s., and are clearly different from our material and appear to be unrelated to it.

Periploma is represented by *Periploma topei* Zinsmeister (1984, p. 1525–1526, fig. 10F–G; Stilwell & Zinsmeister, 1992, p. 89, pl. 10, fig. e–i) in the Eocene La Meseta Formation just off the Antarctic Peninsula. The interior of this shell, however, is unavailable and the shape is reminiscent of the rather quadrate *Thracia meridionalis* E. A. Smith, 1885 (Dell, 1990, p. 63–65, fig. 109–111), an extant circum-Antarctic species. Shell interiors and conjoined specimens are necessary to ascertain the correct generic placement of *Periploma topei*. Other records of fossil Periplomatidae in southern South America are restricted to only six species. *Periploma* (*Aelga*) *primaverensis* Griffin, 1991 (p. 141–142, fig. 10.3–10.6) appears very rarely in Eocene rocks exposed at the southernmost tip of the continent and has been referred to the subgenus *Aelga* Slodkewitsch, 1935 (type species *Tellina bessohensis* Yokoyama, 1924; p. 14, pl. 3, fig. 1–5; Makiyama, 1957, pl. 12, fig. 1–5) because of the sinuous character of its commissure in ventral view. The second record is a specimen illustrated herein—probably belonging in a new species—coming from the late Oligocene-early Miocene Monte León Formation exposed at Punta Beagle, a few kilometers upstream from the mouth of the Santa Cruz River, in southern Patagonia. The preservation of the sole specimen is too poor to warrant full description, but it apparently belongs in *Offadesma,* becoming thus the earliest representative of this subgenus in South America.

The third record—i.e., the new species described herein—is from Miocene rocks that outcrop along the coast of northern Patagonia and is the first one of the genus in Neogene deposits here, despite the fact that the faunas included in them are very diverse and well known. This testifies to the rarity of this taxon, which has obviously been overlooked during previous collecting in the area.

The other three nominal species referable to the Periplomatidae were described from Tertiary localities along the Pacific coast of Chile. These are "*Anatina*" *suborbicularis* Philippi, 1887 (p. 154, pl. 33, fig. 2) from Millanejo, "*Anatina*" *davilae* Philippi, 1887 (p. 155, pl. 33, fig. 1) from Levu and "*Anatina*" *araucana* Philippi, 1887 (p. 155, pl. 23, fig. 14) also from Levu. Only "*Anatina*" *suborbicularis* may be possibly referable to *Offadesma*. "*Anatina*" *davilae* is a closed shell with damaged edges and apparently lacks an umbonal slit. This seems to preclude its inclusion even in *Periploma*. "*Anatina*" *araucana* is represented by an internal mold with only fragments of the shell adhered to it, and it is practically unidentifiable.

GEOLOGY

In the area surrounding Punta Pardelas (Figure 10) there are numerous exposures of rocks referred to as the Puerto Madryn Formation (Haller, 1978), a marine unit that has yielded an abundant and diverse mollusk fauna known from the earliest years of the Twentieth Century (e.g., Ihering, 1907; Brunet, 1995, 1997; del Río & Martínez Chiappara, 1998 and references therein). The lithostratigraphic unit comprises about 90 meters of sandstone and siltstone representing the widespread marine transgression that occurred at the end of the Miocene covering large areas of southern South America (Frenguelli, 1920, 1926, 1947; Camacho, 1967; Aceñolaza, 1976; Irigoyen, 1969; Haller, 1978; Herbst & Zabert, 1987; del Río, 1992, 1994, 2000 and references therein). Previous paleoenvironmental work by Scasso & del Río (1987) suggested a near-shore shelf environment for these deposits in the Puerto Madryn area. A sequence stratigraphic study by del Río et al. (2001), allowed discrimination of a number of different cycles representing diverse shell accumulations reflecting changes in sea level and environments. The age of the Puerto Madryn Formation was believed to be Late Miocene based on its fossil content (del Río, 1988, 1992), K/Ar dating (Zinsmeister et al., 1981) and Sr^{87}/Sr^{86} dating (Scasso et al., 1999).

At Punta Pardelas, only about 20 meters of the total thickness of the Puerto Madryn Formation are exposed. They include a bottom bed of gray mudstone with an abundant and well preserved invertebrate fauna (6.5 m), overlain by very hard yellowish tuffaceous sandstones (3.5 m), a very fine gray sandstone with abundant molluscan shells and echinoids (4 m), a yellow fine sandstone with abundant mollusks and echinoids (1 m), yellowish laminated mudstones with intercalated gypsum beds (6 m) and cross-bedded light brown calcareous sandstone with abundant invertebrates. The material described herein comes from the fine yellow sandstone at 15 meters above the base of the exposed section.

The specimen of *Offadesma* n. sp. illustrated in Figure 3 comes from the Monte Entrada Member of the Monte León Formation, exposed at Punta Beagle, about 15 km inland from the mouth of the Santa Cruz River, at its junction with the Chico River, province of Santa Cruz, Argentina, southern Patagonia. The Monte León Formation (Bertels, 1970, 1980) comprises about 200 m of sandstone, siltstone and tuffaceous sandstone with a very diverse, abundant and well preserved mollusk fauna (Ihering, 1897, 1907, 1914; Ortmann, 1902; del Río & Camacho, 1998, among others). The restricted outcrop at Punta Beagle includes only 10 to 12 meters of silty sandstone, topped by a 60 cm oyster bank overlain by a hard and massive yellow sandstone from where the specimen was collected. The age of the Monte León Formation has been subject to controversy, but is generally accepted as latest Oligocene-earliest Miocene (Bertels, 1980; Náñez, 1990; Legarreta & Uliana, 1994; del Río & Camacho, 1998; Barreda & Palamarczuk, 2000).

All specimens described are housed in the Museo Paleontológico Egidio Feruglio (MEF-Pi), Trelew, Argentina and the University of La Pampa (GHUNPam), Santa Rosa, Argentina.

SYSTEMATICS

Class Bivalvia Linné, 1758

Subclass Anomalodesmata Dall, 1889

Order Pholadomyoida Newell, 1965

Superfamily THRACIOIDEA Yonge & Morton, 1980

Family PERIPLOMATIDAE Dall, 1895

Genus *Offadesma* Iredale, 1930

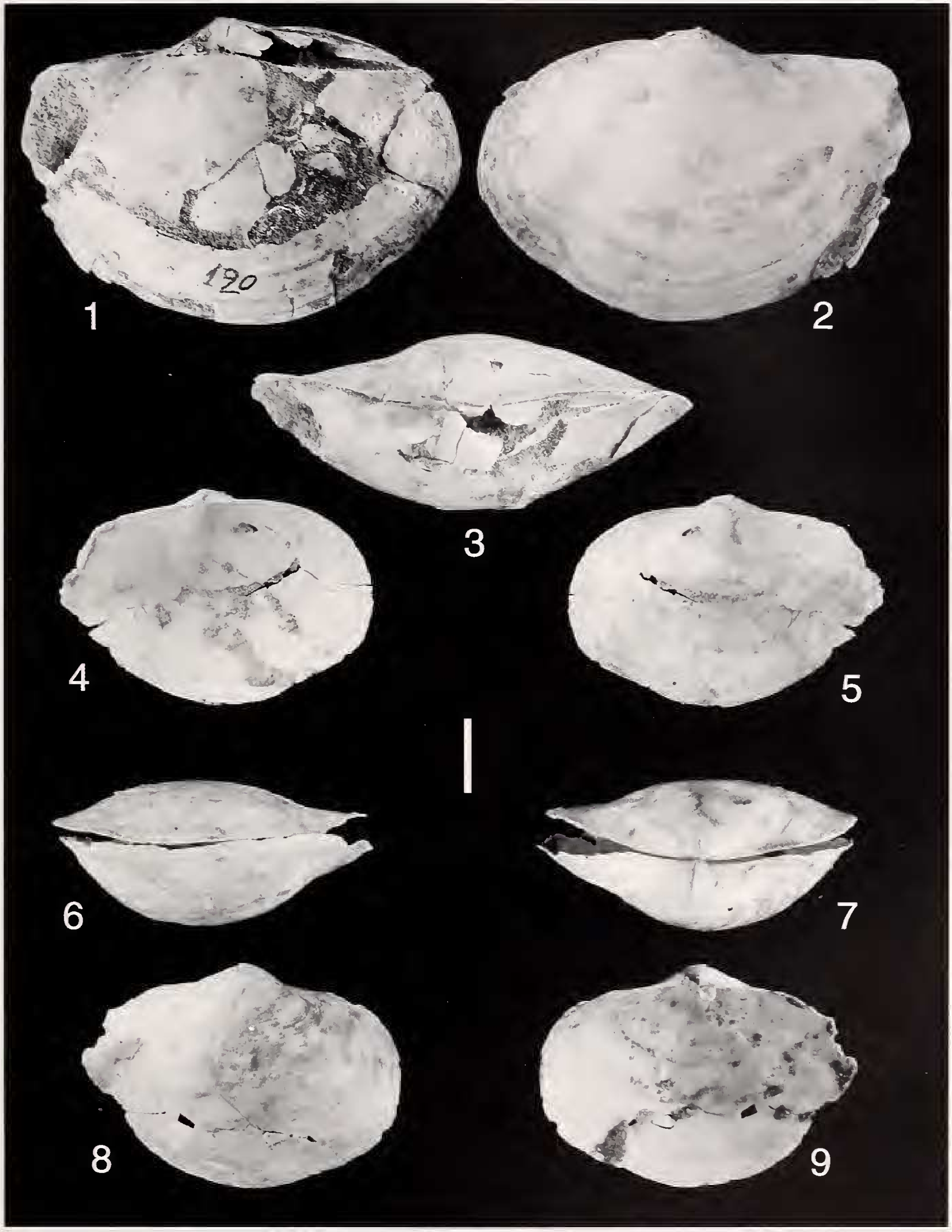
Type species: *Offadesma angasi* Crosse & Fischer, 1864.

Remarks: *Offadesma* has been considered a subgenus of *Periploma* Shumacher, 1817 by various authors (Keen, 1969), while others considered it a distinct genus within the family (Rosewater, 1968; Fleming, 1950). The much more pronouncedly inequivalve shells, the posteriorly inclined chondrophore with poorly developed anterior and posterior outer ligaments, and the entirely missing lithodesma seem to warrant generic distinction (Fleming, 1950; Coan et al., 2000).

Offadesma isolatum Griffin & Pastorino sp. nov. (Figures 1–9)

Diagnosis: Medium sized *Offadesma* (height about 40 mm, length about 60 mm) with chondrophore strongly directed postero-ventrally, anterior margin somewhat produced, right valve inflated (about 25% more than left valve), posterior rostrum occupying 28–30% of total shell area.

Description: Shell strongly inequivalve, inequilateral, very thin, about 60 mm long and 40 mm high; right valve deeply cup-shaped; left valve gently convex; right umbo



Figures 1–9. *Offadesma isolatum* n. sp. Figures 1–3. holotype MPEF-PI 190. left, right and umbonal views. Punta Pardelas. Chubut. Argentina. Puerto Madryn Formation. Figures 4–9. paratype. MPEF-PI 191 Figure 4–5. Internal and external views of the left valve. Figures 6–7. Ventral and dorsal views of the same specimen. Figures 8–9. External and internal views of the right valve. Scale bar = 1 cm.

arched over left one; anterior margin rounded, narrowly gaping anteroventrally; posterior margin rostrate, truncated and slightly directed upwards and leftwards; rostrum slightly gaping; weak oblique ridge running from umbo to base of anterior margin; broader and slightly stronger ridge extending from umbo to base of posterior truncation; area between posterior ridge and dorsal border of shell apparently covered by fine sand grains which are impressed on the shell surface; transverse umbonal crack present, running perpendicular to dorsal antero-posterior axis of shell for about 10% of total height; anterior edge of crack overlying posterior edge; primary ligament in deep spoon-shaped chondrophore directed postero-ventrally; anterior outer lamellar ligament running in short moderately deep slit for about dorsal fourth of total height of inner fibrous ligament; posterior outer lamellar ligament in slightly wider and longer slit; chondrophores supported by clavicles extending from the posterior face of chondrophore in postero-ventral direction; chondrophores unequally aligned vertically, displaced to the right into the cup-shaped right valve; adductor muscle scars and pallial line unknown; external surface carrying weak and regularly spaced commarginal ribs and growth lines evident in the intercostal spaces.

Type locality: The material comes from Punta Pardelas in Península Valdés, northeastern Chubut, Patagonia, Argentina. All specimens come from rocks included in the late Miocene Puerto Madryn Formation.

Type material: Holotype, MEF-Pi-190a, a bivalved specimen (valves loose); paratype, MEF-Pi-190b a bivalved shell, partly broken.

Remarks: This species closely resembles *Offadesma marwicki* Fleming, 1950 (p. 246–247, pl. 24, fig. 10). The type specimens come from Black Point in the Waitaki Valley, New Zealand, where they were collected in late middle Eocene (Bortonian) rocks. Fleming also mentions this species from the Pahi Greensands in North Auckland, also Bortonian in age; these are the earliest record of *Offadesma.* As in the material from Punta Pardelas, the shell is not quite as strongly inequivalve as in the type species, which has a more inflated left valve. The New Zealand specimens seem to be slightly smaller and the umbos are more prominent than in our material.

Offadesma angasi (Crosse & Fischer, 1864) lives presently along the coast of southeastern, south and southwestern Australia and also in New Zealand (Rosewater, 1968; Morton 1981a). The only apparent difference with *Offadesma isolatum* n. sp. is that the shell in the type species is more strongly inequivalve and the anterior margin of the shell is more evenly rounded.

Offadesma sp. (Marwick, 1931, p. 83, fig. 110–111; Fleming, 1973, pl. 64, fig. 720–721) from the Kapitean (late Miocene) of New Zealand is very similar, except perhaps in that the shell is more strongly inequivalve.

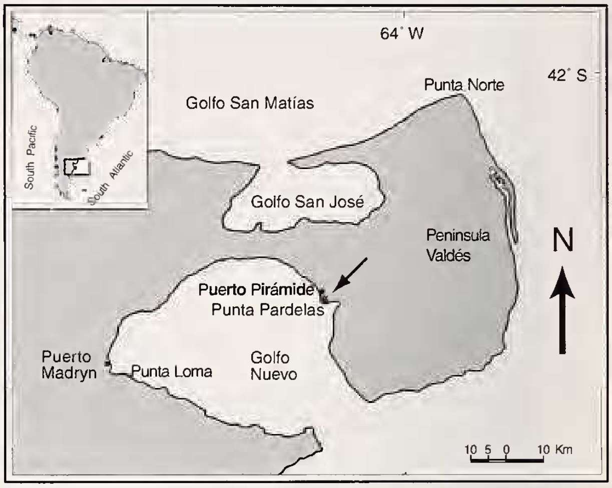


Figure 10. Location map of the fossil locality in the Valdés Peninsula area, Argentina.

Unfortunately, the interior of the material described by Marwick is not visible for further comparison.

Of the three species of Periplomatidae described by Philippi (1887) from Tertiary rocks in Chile, none show the interior of the shells. Therefore their inclusion in *Offadesma* (and in two cases even in *Periploma*) is at present at least doubtful. The species that most closely resembles ours in shape is "*Anatina*" *suborbicularis* Philippi, 1887 (p. 154, pl. 33, fig. 2). However, it is much higher and apparently the posterior end of the shell is less clearly defined and the posterior gape is much narrower than in *Offadesma isolatum* n. sp.

Other species of Periplomatidae from South America can not be compared with our material. They all fall within *Periploma* s.s. and their differences with *Offadesma* are readily clear. Such is the case of the extant species from the Caribbean and northern South America *Periploma* (*Periploma*) *coseli* Ardila & Díaz, 1998 (p. 69–71, Fig. 1–2, 5) and *Periploma* (*Periploma*) *sanctamarthaensis* Ardila & Díaz, 1998 (p. 72, Fig. 3–4, 6). These are missing the distinctive backward pointing chondrophore and the posterior rostrum of *Offadesma,* which are clearly visible on our specimens. Likewise, the west African record of this genus, i.e. *Periploma camerunensis* Cosel, 1995 (p. 102–110, figs. 144–145) is also very different from *Offadesma,* while it appears to be quite close to the Caribbean species.

Etymology: From the Latin *isolatum* = detached, separate, in allusion to its isolate occurrence from other records of the genus.

Offadesma sp.
Figures 11–13

Material: One specimen, partly decorticated and somewhat crushed (GHUNLPam26300).

Figures 11–13. *Offadesma* sp. (GHUNLPam26300) from Punta Beagle, province of Santa Cruz, southern Patagonia, Argentina, Monte Entrada Member of the Monte León Formation. Scale bar = 1 cm.

Occurrence: Punta Beagle, province of Santa Cruz, southern Patagonia, Argentina (49°57′S 68°41′W). The specimen was found within the Monte Entrada Member of the Monte León Formation, at the top of the exposure of this unit in Punta Beagle.

Remarks: The only specimen available is somewhat deformed and the margins too broken to allow proper description or even accurate comparisons with other taxa. However, what is visible of its hinge shows a chondrophore that leaves no doubt it is an *Offadesma.* It is smaller and slightly more rounded than *Offadesma isolatum* n. sp. from the Puerto Madryn Formation. The significance of this material lies in that it is the earliest record of the genus in South America.

BIOGEOGRAPHIC HISTORY OF *OFFADESMA*

The living species of *Offadesma* are restricted to Australia and New Zealand, while *Periploma* s.s. is known to occur along both coasts of the American continent (including the coast along northern Patagonia) and along the western coast of tropical Africa (Cosel, 1995). The presence of *Periploma* in Africa can be easily explained through passive dispersal of larvae across the Atlantic in an eastwards direction by means of the Equatorial Undercurrent or the Equatorial Countercurrent. The role of these marine currents in passive dispersal of larvae of different groups of mollusks in the tropical Atlantic Ocean has been discussed by Scheltema (1995). Morton (1981a) assumed a short planktonic period for the larvae of *Offadesma,* based on the size of the eggs and comparisons with other anomalodesmatans. He even suggested that the eggs may be incubated in the ctenidia, although admitting that there is no evidence for this. While the larval development of this genus remains obscure and further research is needed to assess its role in the geographic distribution of its species, the evidence provided by the fossil record suggests that it was far more widespread earlier in the Cenozoic than at present. No larval stages are known for fossil forms, but it could be possible that with increasing specialization and concomitant occupation of narrower niches, a shortening in the duration of larval stages would ensure the rapid development crucial to ensure rapid colonisation of difficult environments.

In Patagonia, the family is represented by *Periploma ovatum* d'Orbigny, 1846 (p. 514, pl. 81, fig. 10–12) and *Periploma compressum* d'Orbigny, 1846 (p. 514, pl. 78, fig. 19–20), both ranging from (northern?) Brazil to northernmost Patagonia. As already stated, although all these species undoubtedly belong in *Periploma,* their shell characters show that they are unrelated to the Indo-Pacific *Offadesma* and thus to *Offadesma isolatum* n. sp. from the Puerto Madryn Formation. The two extant species from the southwestern Atlantic seem to be closely allied to the Caribbean taxa mentioned above. This leads to the presumption that the origin of the two living taxa must lie in a southward migration of Caribbean fauna as proposed by del Río (1991) and Martínez Chiappara &

del Río (2002). This migration would have been responsible for the development of the Valdesian and Paranaian Malacological Provinces (Martínez Chiappara & del Río, 2002) along the coasts of the southernmost tip of South America during the late Miocene. Although the southward flowing Brazil current could have played a role in the dispersal of larvae along the coast of South America, it was probably far more important in the establishment of appropriate ecological conditions for the settlement of species from warmer water. These species could have extended or restricted their southward range merely by occupying or vacating progressively warmer or colder areas at the southernmost extreme of their distribution as the influence of the Brazil Current varied with the evolving circulation pattern in the South Atlantic during the Cenozoic. The warmer conditions that enabled the development of the provinces proposed by Martínez Chiappara & del Río (2002) would have been caused—according to them—by a temporary blocking of the Antarctic Circumpolar Current (ACC) due to the appearance of the Scotia volcanic arc. This, together with the fact that the cold northwards-flowing Malvinas Current (MC) was not fully developed yet, would have been the main cause of the warming of the surface water in northern Patagonia. Nevertheless, Martínez Chiappara & del Río (2002) suggested that a proto-MC may have been to some extent already influencing the conditions in the area during the late Miocene, as indicated by the fossil content of some of the shell bearing beds in the Puerto Madryn Formation.

At any rate, some elements of the Miocene fauna from the Puerto Madryn Formation could possibly have originated elsewhere. It is well known that the opening of Drake Passage was crucial in the development of the present marine circulation pattern in the southern oceans. This opening probably occurred at the end of the Oligocene (23.5 ± 2.5 Ma; Barker & Burrell, 1977, 1982), although it could have been a long process beginning as far back as 37 Ma (Crame, 1999). The consequent onset of the ACC—and its intensification with the beginning of glaciation in West Antarctica just before the end of the Miocene (Kennet et al., 1975; Kennet, 1977; Kennet & von der Broch, 1985)—provided a gateway for the migration of many mollusk genera from New Zealand eastwards to South America and from South America eastwards to Australasia. Examples of such migrations are many (Beu & Griffin, 1996; Beu et al., 1997) and taxonomic work on the Patagonian faunas may prove that there are even more cases that have been overlooked. One of these could be the case of *Offadesma isolatum* n. sp. The rarity of this species due to its fragile shells and restricted habitat (Morton, 1981b) could explain why it has not been previously mentioned in the Patagonian fossil record. The affinities of the new species described herein seem to lie with Indo-Pacific taxa ranging back into the Paleogene. While yet unclear and possibly subject to change with further collection, the fossil record and present distribution of *Offadesma* point towards a southern Indo-Pacific origin. Although the fossil record of this genus is very poor, its appearance in New Zealand as early as the Bortonian (late middle Eocene) appears to be consistent with its present distribution and the only discordant records are the early and late Miocene South American occurrences. While acknowledging its poor chances of preservation, the absence of *Offadesma* from Cenozoic rocks anywhere in North, Central or elsewhere in South America suggests that its presence in the early Miocene Monte León Formation and the late Miocene Puerto Madryn Formation is unlikely to be caused by its southern migration from warmer water further north along the Atlantic coast. More plausible seems to be its arrival in southern South America as a consequence of dispersal by means of the ACC. The fact that it appears earlier in New Zealand is consistent with the postulated Indo-Pacific origin of the genus. The chances of passive dispersal of larvae in an eastwards direction from New Zealand to South America—rather than from South America to New Zealand—would be enhanced by the shorter distances involved and the increased speed of the ACC during the Miocene. The distribution of some mollusks common to South America and New Zealand/Australia is still poorly understood. However, it may be possible that migration between both areas occurred repeatedly throughout the Cenozoic in *both* directions, even as recently as the late Pleistocene, when the bivalve *Anadara trapezia* suddenly appeared in New Zealand (OIS11) and Australia (OIS7), probably descending from a South American ancestor (Beu & Griffin, 1995; Beu et al., 1997; Murray-Wallace et al., 2000).

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